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Artículo Original

FOOT ANATOMY OF *Chaetomys subspinosus* (CAVIOMORPHA, ERETHIZONTIDAE): ITS SIGNIFICANCE FOR UNDERSTANDING THE EVOLUTION OF ARBOREALITY IN NEOTROPICAL PORCUPINES

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ABSTRACT. The porcupine *Chaetomys subspinosus* (the ouriço-preto or thin-spined porcupine), the only species of this genus, is a caviomorph rodent pertaining to the Erethizontidae. This is a strictly arboreal folivorous species, endemic to the Brazilian Atlantic Forest. Despite some contributions to its morphology and biology, its postcranial characters associated with an arboreal lifestyle are poorly known. In this contribution, we performed a morphofunctional study of the foot of *C. subspinosus* and compared it with that of extant and extinct erethizontids. In addition, we evaluated the evolution of the foot anatomy of *C. subspinosus* in the context of the Erethizontidae, reconstructing the ancestral morphology of selected characters with functional significance for climbing. The anatomical and evolutionary analysis of the foot of *C. subspinosus* indicates that certain characters identified as highly specialized for climbing (hypertrophied medial sesamoid, reduced hallux, and medially oriented first metatarsal) would have evolved independently in the extant Neotropical porcupines. This set of characters constitutes a noticeable case of postcranial homoplasy related to the evolution of arboreal habits in caviomorphs.

RESUMEN. ANATOMÍA DEL PIE DE *Chaetomys subspinosus* (CAVIOMORPHA, ERETHIZONTIDAE): SU SIGNIFICANCIA PARA ENTENDER LA EVOLUCIÓN DEL MODO DE VIDA ARBÓREO EN LOS PUERCOESPINES NEOTROPICALES. El puercoespín *Chaetomys subspinosus* (ouriço-preto), la única especie del género, es un roedor caviomorfo perteneciente a Erethizontidae. Esta especie es estrictamente arbórea, folívora y endémica de la Mata Atlántica brasilera. No obstante la existencia de algunas contribuciones sobre su morfología y biología, sus caracteres poscraneales asociados a un estilo de vida arbóreo son poco conocidos. En esta contribución, realizamos un análisis morfofuncional de la anatomía del pie de *C. subspinosus* y la comparamos con la de otros eretizóntidos actuales y extintos. Además, evaluamos la evolución de la anatomía del pie de *C. subspinosus* en el contexto de los Erethizontidae, y reconstruimos la morfología ancestral de aquellos caracteres funcionalmente significativos para trepar. El análisis anatómico y evolutivo del pie de *C. subspinosus* indica que ciertos caracteres identificados como altamente especializados para trepar (sesamoide medial hipertrofiado, *hallux* reducido y primer metatarsiano medialmente orientado) habrían evolucionado de manera independiente en los puercoespines neotropicales actuales. Este conjunto de caracteres constituye un notable caso de homoplasia en el poscráneo de los caviomorfos, relacionado con la evolución de los hábitos arborícolas en estos roedores.

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Key words: Arboreal lifesyle, Chaetomyinae, foot morphology, evolutionary convergences.

Palabras clave: Modo de vida arbóreo, Chaetomyinae, morfología del pie, convergencias evolutivas.

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INTRODUCTION

The Erethizontidae, known as New World porcupines, are a clade of caviomorph rodents currently represented by the Neotropical genera *Coendou* and *Chaetomys* and the Holarctic *Erethizon* (Voss et al. 2013; Voss 2015). During their evolutionary history in South America, porcupines reached a high taxonomic diversification, represented by at least eight extinct genera (Ameghino 1887; Candela 1999, 2000, 2003; Vucetich & Candela 2001; Candela & Vucetich 2002; Boivin et al. 2017; Ercoli et al. 2021). In the Neotropical Region, the porcupines mainly inhabit forests of different types, but they are also found in more open biomas, such as the Cerrado and the Caatinga (e.g., Voss 2015). Unlike *Coendou*, which includes about 15 species (Voss et al. 2013; Menezes et al. 2021), *Chaetomys* contains only one species, the ouriço-preto or thin-spined porcupine *C. subspinosus*, which is endemic to the Brazilian Atlantic Forest, ranging from southeastern Espirito Santo to central-eastern Sergipe (Giné & Faria 2018). *Chaetomys subspinosus* is a relatively small (body mass about 1.6 kg) highly arboreal porcupine, with nocturnal and solitary habits (Chiarello et al. 1997) and a folivorous diet, almost exclusively based on leaves of woody trees (Giné et al. 2010; Lima 2010). Originally, *Chaetomys* was considered within Erethizontidae (e.g., Thomas 1897; Ellerman 1940), but it was later classified as an Echimyidae (e.g., Miller & Gidley 1918; Patterson & Wood 1982). Currently, strong evidence supports its inclusion within Erethizontidae (Martin 1994; Carvalho 2000; Vilela et al. 2009; Voss et al. 2013). *Chaetomys* is contained within its own subfamily, Chaetomyinae, which is recovered as a basal taxon to the *Coendou–Erethizon* clade, representing an early erethizontid radiation, possibly originated in the Early Miocene (Vilela et al. 2009; Voss et al. 2013; Boivin et al. 2019). Among the morphological characters of *C. subspinosus*, its postcranial anatomy is poorly known, in part probably due to the scarce specimens housed in museum collections. It has been previously mentioned that *C. subspinosus* has a specialized pes similar to that of *Coendou* (Waterhouse 1848; Ellerman 1940), and some of its characters have been pointed out in comparative studies on caviomorphs (Candela & Picasso 2008; Candela et al. 2017). However, its autopodial anatomy has not been analyzed in detail from an evolutionary or functional point of view.

In this contribution, we studied the foot anatomy of *C. subspinosus* and compared it with that of extant and extinct erethizontids. On this basis, we assessed its implications in the understanding of the evolution of the climbing ability and arboreal lifestyle in Erethizontidae.

MATERIALS AND METHODS

We compared the foot anatomy, focusing on the tarsal-metatarsal region, of *Chaetomys subspinosus* with that of the extant *Coendou prehensilis*, *C. spinosus*, *Erethizon dorsatum*, and the extinct Early Miocene Patagonian *Steiromys duplicatus* (Appendix 1). Information on the foot of *S. duplicatus* was also taken from Scott (1905) and Candela & Picasso (2008). We also revised published information on the foot anatomy of hystricognath rodents provided by Waterhouse (1848), Ellerman (1940), Jones (1953), Gupta (1966), Hildebrand (1978), Grand & Eisenber (1982), Candela & Picasso (2008), and Candela et al. (2017). We performed a morphofunctional study by evaluating the relationships between the tarsal-metatarsal anatomy and the possible movements of the foot (Jones 1953; Hildebrand 1978; McEvoy 1982; Candela et al. 2017) and considering the locomotor behavior and substrate preferences of the analyzed erethizontids: *Coendou* and *Chaetomys* as climbing and arboreal; *Steiromys* and *Erethizon* as climbing and scansorial (Roze 1989; Nowack 1991; Candela & Picasso 2008; Voss 2015). Anatomical nomenclature follows that of Candela et al. (2017) and is illustrated in **Figure** 1. To investigate the evolution of the foot anatomy among porcupines, we reconstructed the ancestral morphology of three characters that showed an important functional significance for climbing (degree of development of the medial sesamoid, size of the hallux, orientation of the metatarsal I; see Appendix 2 for character state definitions). The evolution of the characters was mapped on the phylogeny by Voss et al. (2013) but including *S. duplicatus* following Candela (2000, 2004) and Boivin et al. (2019). The African hystricognath *Hystrix* and the cavioid *Cavia* were used as outgroups (*Hystrix* selected as the root). The resultant data matrix is provided in Appendix 3. Character mapping was evaluated under parsimony using TNT 1.5 (Goloboff & Catalano 2016).

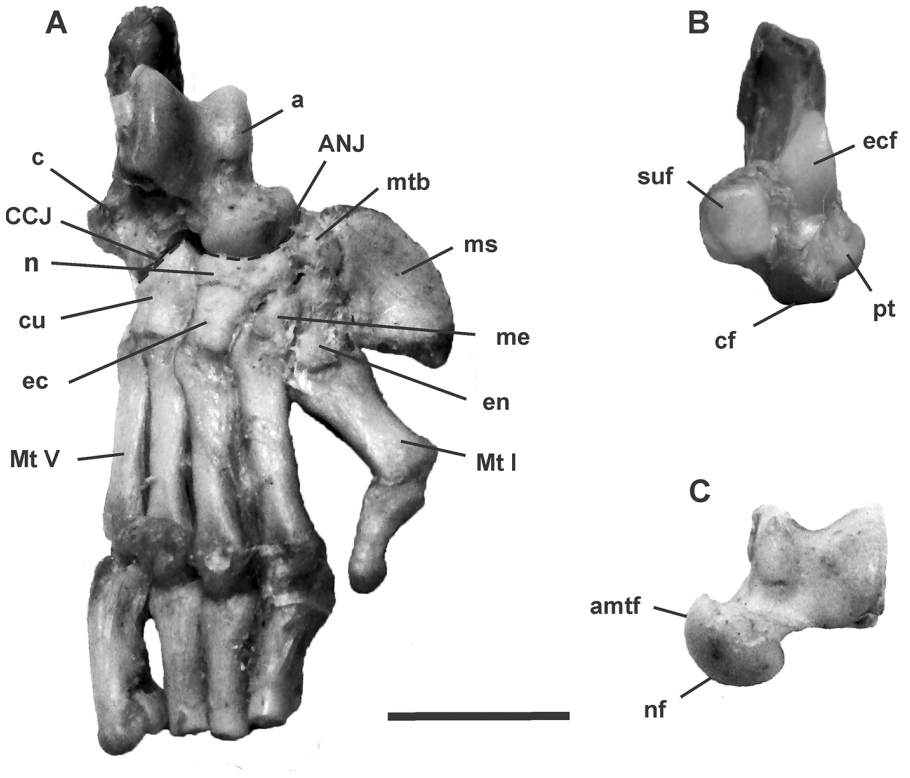

Fig. 1. Foot of *Chaetomys subspinosus* (MN 9680). **A.** Right foot in dorsal view (proximal phalanges II-IV are cut at their distal ends; the medial sesamoid bone is displaced distally, compare with **Fig**. 2A). **B.** Left calcaneus in dorsal view. **C.** Left astragalus in dorsal view. Abbreviations: a: astragalus; amtf: astragalomediotarsal facet; ANJ: astragalonavicular joint; c: calcaneus; CCJ: calcaneocuboid joint; cf: cuboid facet; cu: cuboid; ec: ectocuneiform; ecf: ectal facet; en: entocuneiform; me: mesocuneiform; ms: medial sesamoid; mtb: medial tarsal bone; Mt I, Mt V: first and fifth metatarsals; n: navicular; nf: navicular facet; pt: peroneal tubercle; suf: sustentacular facet. Scale bar: 10 mm.

RESULTS

Our comparative study indicated that the tarsus of *Chaetomys* is relatively wide and similar to that of other erethizontids (**Figs**. 1 and 2). The sustentacular and cuboid facets of the calcaneus are very close together, so that the distal portion of this bone is extremely short (**Fig**. 1B). The sustentacular facet is quadrangular-shaped, and it is oriented almost parallel to the main axis of the calcaneus. The ectal facet is convex and proximodistally oriented, facing medially towards the sustentacular facet. The peroneal tubercle is well-developed, extending from the level of the distal edge of the ectal facet to almost the cuboid facet. The astragalus (**Fig**. 1C) is relatively wide and similar to that of other erethizontids. The astragalar trochlea is asymmetrical, with the lateral astragalotibial facet more lateromedially extended and proximo-distally larger than the medial one. The astragalar head is relatively large and strongly medially oriented with respect to the proximo-distal axis of the foot. The astragalar neck is relatively short. The navicular facet of the astragalar head is very convex and continuous medially with a large astragalomediotarsal facet for the medial tarsal bone. The astragalonavicular joint (ANJ) and calcaneocuboid joint (CCJ) are located approximately at the same level, resulting in a sigmoid transverse tarsal joint. The navicular is proximodistally short. The medial tarsal bone is proximodistally extended, with a concave facet that completely wraps the astragalomediotarsal facet of the astragalus. The cuboid is larger than the ectocuneiform. This latter bone is obliquely oriented with respect to the longitudinal axis of the metatarsal III (Mt III), with its distal facet facing laterally. The mesocuneiform is the smallest of the cuneiforms, and it is obliquely oriented as the ectocuneiform. The entocuneiform

is subrectangular-shaped, extending distally beyond the level of the distal border of the ectocuneiform. As in *Coendou*, but unlike *E. dorsatum* and *S. duplicatus* (Scott 1905; Candela & Picasso 2008), the medial sesamoid of *Chaetomys* is a hypertrophied and flat bone, extending the medial edge of the foot. *Chaetomys* has five well-developed metatarsals that are relatively more gracile and elongated than those of *Coendou* and *Erethizon* and similar to those of *S. duplicatus*. The first metatarsal (Mt I) is robust and medially oriented with respect to the other metatarsals. As in *Coendou*, but unlike *E. dorsatum* and *S. duplicatus*, the hallux is reduced to just the proximal phalanx.

Results of the character foot mapping on the phylogeny of erethizontids (**Fig**. 3) indicate that the feet of *Chaetomys* and *Coendou* show three homoplastic character states: a hypertrophied medial sesamoid (character state 1^2), a reduced hallux (character state 2^1), and a medially deflected Mt I (character state 3^1).

DISCUSSION

In general terms, as in other erethizontids, the tarsus of *Chaetomys* shows the typical characters recognized in the Tarsal-Metatarsal Pattern I (sensu Candela et al. 2017), which is characterized by features that facilitate a wide range of movements at different levels of the tarsal-metatarsal complex. Particularly among extant Neotropical porcupines, the hypertrophied medial sesamoid, the medially oriented Mt I, and the reduced hallux constitute a set of specialized features that is functionally related to grasping ability and inversion movements (Jones 1953; Hildebrand 1978; McEvoy 1982). In addition, the medially oriented astragalar head, the obliquely orientated ectocuneiform, and the ANJ and CCJ located at the same level allow inversion-eversion movements of the foot (Candela & Picasso 2008; Candela et al. 2017). Perhaps the most distinctive feature of the foot of *Chaetomys* and *Coendou* is the hypertrophy of the medial sesamoid, like a "panda's thumb" (Abella et al. 2015) but located in the foot. In *C. prehensilis*, the hypertrophied medial sesamoid is part of a sophisticated complex of movements of the foot related to its climbing ability (McEvoy 1982). These movements are generated by an anatomical functional complex constituted by bones, cartilages, muscles, tendons, and soft tissues (Jones 1953; Hildebrand 1978; McEvoy 1982). The medial side of a large fleshy plantar pad opposes to the rest of the foot by gripping through a downward folding motion, marking a crease line in the integument of the sole (Jones 1953). This medial part includes the reduced hallux and the medial sesamoid, which bears a crescent-shaped cartilage on its free border (Jones 1953; Hildebrand 1978; Grand & Eisenber 1982). The medial sesamoid is active during pedal grip, thus functionally replacing the reduced hallux. The plantaris brevis (attached to the medial sesamoid and a plantar tendon) and adductor ossis sesamoideus medialis (attached to the medial sesamoid and the first metatarsal) muscles act synergistically to generate the medial folding motion of the preaxial plantar pad (Jones 1953; Hildebrand 1978; McEvoy 1982). Therefore, the medial sesamoid acts as a first toe, compensating and functionally replacing the reduced hallux (Jones 1953; McEvoy 1982; Grand & Eisenber 1982). As the anatomy of the foot of *C. subspinosus* is very similar to that of *Coendou*, it allows us to infer a comparable grasping mechanism produced by a similar muscular action in this species.

The generalized condition of the foot in extant erethizontids can be seen in *E. dorsatum*, which has the Mt I parallel to the other metatarsals, a well-developed hallux, a large but non-hypertrophied medial sesamoid, and a smaller plantar pad without the sole crease line (Jones 1953; McEvoy 1982). According to McEvoy (1982), a true "grasping" mechanism of the substrate probably does not occur in *E. dorsatum*. The anatomy of the foot of *S. duplicatus* is similar to that of *E. dorsatum*, suggesting a comparable function of the foot in this extinct species (Candela & Picasso 2008).

Among caviomorphs, *Chaetomys* and *Coendou* are the only taxa exhibiting a hypertrophied medial sesamoid in the foot. Moreover, they constitute two of the few cases of great enlargement of this bone in rodents (Hildebrand 1978). Note that a greatly enlarged medial sesamoid has been observed in different rodent taxa with diverse locomotor habits and that a clear correlation between the presence and size of this bone and locomotor adaptations could not be established (Hildebrand 1978).

On the other hand, the relatively longer metatarsals of *C. subspinosus* with respect to those of *C. prehensilis* are a noticeable difference in the foot of these species. The longer metatarsals of *C. subspinosus* would indicate more agile movements during climbing in this species since more gracile bones decrease limb inertia, increasing rotational velocity and stride rate (Hildebrand 1985; Samuels et al. 2013).

Considering the basal phylogenetic position of *Chaetomys* as the sister taxa of the *Steiromys* (*Erethizon-Coendou*) clade, the optimization of char-

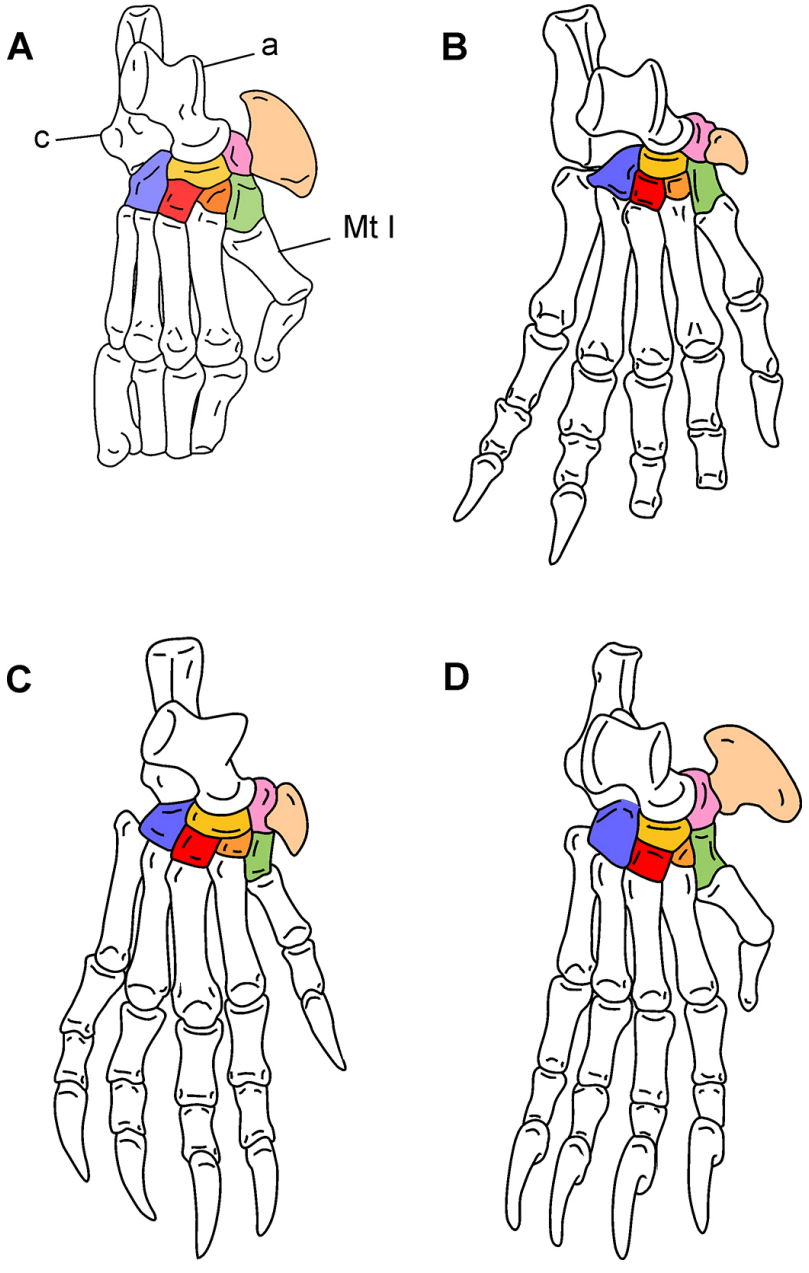

Fig. 2. Dorsal view of the right foot of erethizontids (not to scale). **A.** *Chaetomys subspinosus* (MN 9680). **B.** *Steiromys duplicatus* (reflected; after (Scott 1905). **C.** *Erethizon dorsatum* (MLP 1086). **D.** *Coendou prehensilis* (MLP 1084). Abbreviations: a: astragalus; c: calcaneus; Mt I: first metatarsal. Colour codes: navicular: yellow; medial tarsal bone: pink; medial sesamoid: sand; cuboid: blue; ectocuneiform: red; mesocuneiform: orange; entocuneiform: green

acter states indicates that the specialized foot of *Chaetomys* and *Coendou*, characterized by a hypertrophied medial sesamoid, a reduced hallux, and a medially deflected Mt I, would have been acquired independently (**Fig**. 3). The foot of *Chaetomys* and *Coendou* represents a remarkable example of evolutionary convergence among caviomorph postcranial features. The early divergence of *Chaetomys* with

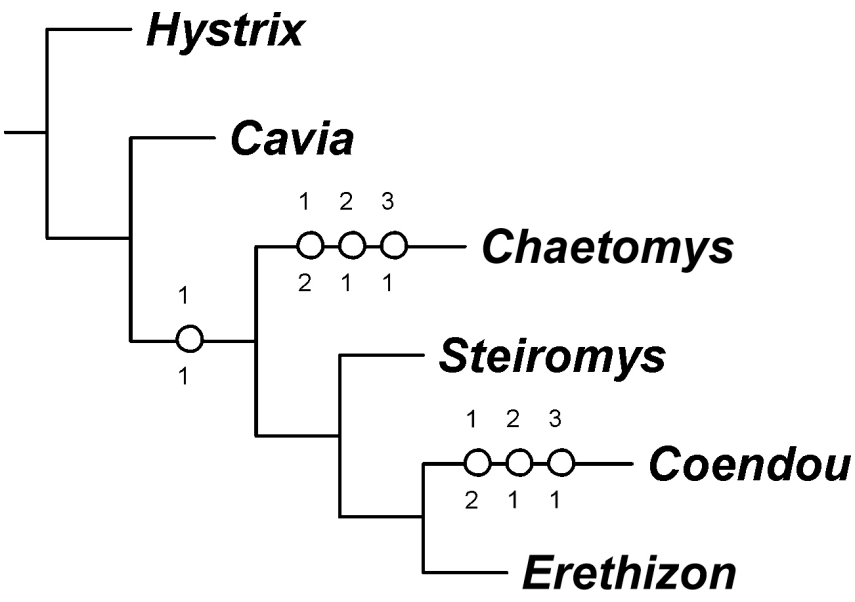

Fig. 3. Mapping of three anatomical characters (see Appendix 2 for character state definitions), as reconstructed using parsimony, onto a composite phylogeny of erethizontids modified from Voss et al. (2013), Candela (2004), and Boivin et al. (2019). Numbers above branches indicate character numbers; numbers below branches indicate character states.

respect to the remaining erethizontids indicates that the lineage of this genus would have had a long evolutionary history, at least since the Early Miocene (Vilela et al. 2009; Voss et al. 2013). We do not know since when the specialized foot of *Chaetomys* was acquired, but this acquisition probably was associated with its high climbing ability. Consequently, similar selection pressures linked with an arboreal lifestyle could have triggered the independent origin of the specialized foot of extant Neotropical porcupines. On the other hand, the foot of *Erethizon* and *Steiromys* (Candela & Picasso 2008), with a non-hypertrophied but moderately enlarged medial sesamoid (a potential synapomorphy of erethizontids; **Fig**. 3), seems to indicate an "anticipatory" morphology from which the evolution of the more derived foot of *Chaetomys* and *Coendou* was possible.

Interestingly, other homoplasies have been previously identified within erethizontids. For example, large body size and inflated nasofrontal sinus have been acquired independently in different species of *Coendou* and, notably, these two characters have evolved identically (Voss et al. 2013). The functional significance of the paranasal sinuses of mammals remains uncertain, but they certainly reduce the weight of the skull (Novacek 1993). In the case of Neotropical porcupines, the enlargement of the nasofrontal sinus has been related to a defensive function against predators (Voss et al. 2013). When considering the correlation between body size and nasofrontal sinus inflation, large *Coendou* species have inflated paranasal sinuses, whereas *Chaetomys*, small *Coendou* species, and the large scansorial *Erethizon* have uninflated sinuses (see Voss et al. 2013). These observations indicate that nasofrontal sinus inflation in recent erethizontids is present only in relatively large species that are strictly arboreal. Even the large extinct *Steiromys*, interpreted as a semiarboreal dweller (Candela & Picasso 2008), exhibits uninflated sinuses (Scott 1905). Therefore, we suggest that inflation of the nasofrontal sinuses in erethizontids could also be related to the lightening of the skull weight in large strictly arboreal porcupines.

In sum, the adaptations for climbing of the foot of *Chaetomys* and *Coendou* can be recognized as those most specialized among caviomorphs and perhaps one of the most noticeable cases of homoplasy linked to the evolution of arboreality in this clade.

More information provided by fossil and extant taxa, integrating data from different sources, is necessary for understanding the adaptations of arboreal caviomorphs. On these grounds, *Chaetomys* opens new questions about the evolution of arboreality in this diverse clade of rodents.

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ONLINE SUPPLEMENTARY MATERIAL

Appendix 1 List of specimens studied
Appendix 2 Character state definitions
Appendix 3 Data matrix